THE EFFECTS OF *PARIDOTEA RETICULATA* ON *GRACILARIA GRACILIS* IN SUSPENDED RAFT CULTURE

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CONTENTS

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ABSTRACT

Large populations of epiphytic *Ceramium* sp. are found in association with commercially farmed *Gracilaria gracilis,* which may be responsible for decreases in *Gracilaria* productivity and quality. Large numbers of the isopod *Paridotea reticulata* are also found in association with the raft flora, their effects on both *Gracilaria* and *Ceramium* are unknown.

Food preference experiments were conducted on the isopods which were given the choice of either *G. gracilis* or *Ceramium* sp. In addition, feeding rate experiments were performed on isopods consuming *Ceramium or Gracilaria* alone. Data on the population dynamics of *Gracilaria*, *Ceramium* and *Paridotea* on *Gracilaria* rafts were also analysed.

When given the choice, *Paridotea* showed a marked preference for *Ceramium* over *Gracilaria*. Feeding rate experiments indicated that small isopods could consume 0.67 ± 0.58g *Ceramium* (wet weight) per gram of isopod (dry weight) per day. In contrast the amount of *Gracilaria* consumed was negligible.

The greatest densities of *Paridotea* in relation to *Ceramium* alone, occurred when *Ceramium* populations were at their lowest, this is when herbivore pressure must be greatest on *Ceramium*. Once *Ceramium* reaches pest proportions, herbivory has very little effect in controlling the seaweed.

Paridotea has little, if any, negative effects on *Gracilaria* because of their slow grazing rates and the availability of *Ceramium*. Their only significant effects on *Gracilaria* are positive, in that isopods slow the initial growth and spread of *Ceramium*.

Hommersand, 1989). In fact two terete species of gracilarioid algae in the British Isles have long been confused under the name *G. verrucosa* (Fredricq and Hommersand, 1989; Steentoft *et al.*, 1995). These two species form two distinct genera namely *Gracilaria gracilis* and *Gracilariopsis longissima* (Steentoft *et al.*,1995). In an attempt to prevent confusion, a lectotype was selected for *Gracilaria gracilis* and *Gracilariopsis* was neotypified (Steentoft *et al.*, 1995). New descriptions were drawn up for both species with great emphasis being placed on field and vegetative features (Steentoft *et al.*, 1995). The species of *Gracilaria* found in Saldanha Bay is now correctly referred to as *Gracilaria gracilis* (Bird and Kain, 1995)

History and future of the *Gracilaria* Industry in southern Africa

In 1937, Isaac recorded large beach casts of *Gracilaria* in Saldanha Bay which was subsequently reported to be a good source of agar (Isaac *et al.* 1943). In 1956 Isaac estimated these beach casts to be in the region of 1 000 tons dry weight per annum.

In southern Africa, the Saldanha Bay-Langebaan Lagoon system on the west coast of South Africa maintains the only natural populations of *Gracilaria* capable of supporting an agar industry (Anderson *et al.* 1989). This system is located approximately 100km north of Cape Town and since Langebaan Lagoon makes up part of the West Coast National Park, only the Saldanha Bay portion is open to commercial exploitation (Anderson *et al*, 1992).

During the Second World War (1938-1945), agar supplies from Japan were interrupted (Anderson *et al.*, 1989; Critchley and Rotmann, 1992) and *Gracilaria* beach-casts, previously regarded as a public nuisance in the Saldanha Bay area were collected for agar extraction (Simons, 1977). At first, there were about four operators with large labour teams collecting the washed up seaweed. This was marketed through traders in Cape Town to agar producers around the world. In the 1960's, two agar production factories were established in the Cape Province (Rotmann, 1990). By this stage, the *Gracilaria* collecting industry had become extremely successful, earning R1 000 000 in 1973 (Simons, 1977).

The mid 1970's saw the collapse of the *Gracilaria* industry when dredging and marine construction caused a crash in the natural *Gracilaria* populations (Rotmann, 1990). *Gracilaria* beach cast material decreased from 1000 to zero dry tons per annum in 1979 (Rotmann, 1990). The industry recovered significantly after this collapse until the yields reached a peak of 429 dry tons per annum in 1988 (Anderson *et al.*, 1993). Subsequently, the yields fell to zero and recovered to 377.9 t dry weight worth US $ 453 500 in 1993 (Anderson *et al.*, 1996).

Gracilaria farming in Chile is considered to be of social and economic importance (Santelices and Doty, 1989), her *Gracilaria* related revenue being in the region of US $ 35 million in 1990 (Buschmann *et al.*, 1995). Revenue gained in Saldanha Bay through *Gracilaria* is comparatively low but has the potential to be increased significantly. Presently, only beach cast material is collected for the production of agar, however, this does not produce reliable yields. Thus there are no agar producing factories in South Africa. Most *Gracilaria* is exported to Japan, Korea, Chile and Namibia where agar is extracted (Critchley and Rotmann, 1992).

The establishment of an agar factory in Saldanha Bay would provide more jobs and a source of revenue to the area. Another potential area for expansion is the commercial farming of *Gracilaria* which is necessary to support an agar factory. Pilot experiments are presently being run by the Department of Sea Fisheries, to assess the viability of commercial *Gracilaria* farming in Saldanha Bay. Commercial farming would provide jobs as well as stabilise the *Gracilaria* yields and supplement the natural *Gracilaria* population. The farming method implemented is to seed vegetative cuttings of *Gracilaria* from the natural stock on to netting ropes called netlons (Dawes, 1995). These ropes are then suspended from rafts so that the *Gracilaria* is growing 0.5 metres from the water surface (Figure 1). The rafts are anchored to the substrate using concrete blocks. In addition to suspension rafts, *Gracilaria* has also been cultivated in tanks since July 1993 near Port Elizabeth, South Africa, where it is used as the principal source of food for the abalone, *Haliotis midae* Linn. (Smit *et al.*, unpublished).

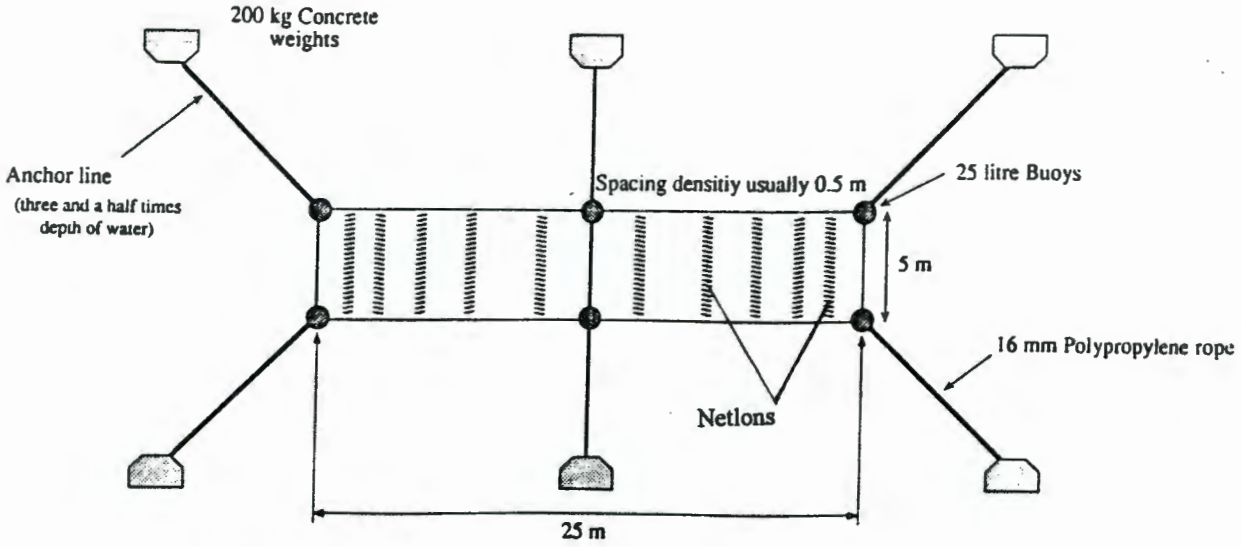

Figure 1. Diagram (plan view) of suspension raft system used in lagoons in Namibia and South Africa (from Dawes, 1995).

The problem of fouling algae and epiphytes

Gracilaria rafts produce large algal monocultures which may create perfect conditions for the settlement and spread of epiphytes. Growth under unnatural conditions may also render the host plant more susceptible to epiphyte establishment (Fletcher, 1995). For example, *Gracilaria* populations on rafts are probably exposed to more intense light conditions than would normally be the case. These unnatural conditions may make *Gracilaria* more susceptible to pest organisms which can ultimately influence the production levels of commercially grown seaweeds (Enright, 1979; Buschmann and Gomez, 1993). Thus, controlling epiphytes in aquaculture can increase seaweed productivity, agar yield and lower production costs.

Epiphytes affect the productivity of their hosts by reducing the amount of light reaching the host plant (Sand-Jensen, 1977; Buschmann and Gomez, 1993), competing for nutrients, dissolved gasses and by adding excess weight to the host which promotes detachment and breakage (Buschmann and Gomez, 1993 and D' Antonio, 1985) .

Buschmann and Gomez (1993) performed experiments which simulated the possible effects of epiphytic algae on the host algae, and found that the most important negative effects of epiphytes were through shading and the addition of excess weight. Competition for nutrients and dissolved gasses played a very small role as an effect detrimental to *Gracilaria*. .

In August 1993, wash ups of *Ulva lactuca* L. occurred in Saldanha Bay (Anderson *et al.*, 1996). Contamination of *Ulva* rendered the *Gracilaria* beach cast useless, which had to be removed at great cost to the local authority (Anderson *et al.*, 1996). Therefore, as well as causing of a losses in the hosts' productivity, large infestations of epiphytes may also lower the quality of the *Gracilaria* cast, making it an uneconomical source of agar. A similar problem was also recorded by Enright (1979), where epiphytic *Ulva* and *Enteromorpha* contaminated the commercial crop *Chondrus crispus* stackh., reducing the yield and quality of the crop.

Many macroalgae have mechanisms to prevent fouling and settlement. These include chemical deterrents (Sieburth and Conover, 1965) and also the sloughing off of the epidermis or cuticle (Moss, 1982). These defences have not been found in *Gracilaria,* which often requires assistance in the control of epiphytes (Fletcher, 1995).

Perhaps the most effective methods of controlling epiphytes are preventative methods and good husbandry. This includes ensuring that pests are removed before planting takes place (Santalices and Doty, 1989), ensuring that sea water is free of contaminants and harvesting before epiphytes become firmly established (Anderson *et al.*, 1992). However, when epiphytes do become established, a commonly used method of removal is their physical removal from the host (Fletcher, 1995). For epiphytes with penetrating rhizoidal filaments, this often involves hand removal which is impractical for large cultures and can damage the host. It is also possible to control epiphytes by manipulating pH (Fletcher, 1995), nutrient concentrations (Pickering *et al.*, 1993) and chemicals such as copper or sodium hyperchlorate (Ugarte and Santilices, 1992), however these methods can only be used successfully for mariculture in confined spaces such as tanks or ponds.

Biological control is another method which has the most potential in tank cultures. There have been many experiments which have shown that grazers often consume epiphytes and could perhaps be used for epiphyte control (Brawley and Fei, 1987 and Duffy, 1990). On the other hand, grazers can be detrimental to crop seaweeds, causing more harm than good (Nicotri, 1977; Shacklock and Croft, 1981). Presently there are very few references to herbivores being used in biological control in marine systems. Those which are being used are fish. The two most common being milkfish (*Chanos chanos* Forsskal) and *Tilapia mossambica* Peters (Chiang, 1981). Both species are used in Taiwan in order to control the epiphytes of pond grown *Gracilaria* (Chaing, 1981). The fish have to be removed from the ponds after the epiphyte population has decreased in order to prevent damage to the *Gracilaria* (Chiang, 1981).

The epiphyte problem in Saldanha Bay

During certain times of year, *Gracilaria* rafts become infested with the epiphytic *Ceramium*. Occasionally, *Ceramium* reaches greater proportions than *Gracilaria* itself, thus lowering the quality of the *Gracilaria* yield. Besides the effects on *Gracilaria* quality, *Ceramium* may also affect *Gracilaria* yields.

Gracilaria rafts in Saldanha Bay are also inhabited by a large numbers of invertebrates. The two most common species of invertebrate are the amphipod, *Jassa falcata* Montagu and the isopod, *Paridotea reticulata* Barnard. *Jassa falcata* is a small amphipod reaching a maximum of 5mm in length, however it can attain extremely high densities of up to 30 000 individuals per 100g dry weight *Gracilaria* (Smit, unpublished data). It is a cosmopolitan species, occurring from Namibia to Natal in Southern Africa (Griffiths, 1976). Brawley and Fei (1987) also found *J. falcata* in association with *Gracilaria asiatica* Zhang and Xia and *Gracilaria lemaneiformis* Bory on a mariculture farm near Quingdao, Peoples Republic of China. In addition to *Jassa*, two epiphyte species were also found on *Gracilaria*, (*Enteromorpha linza L.* and *Scytosiphon lomentaria* Lyngbye). Brawley and Fei (1987) conducted food preference experiments on some of the invertebrate fauna found on the farm including *Jassa*. Results indicated that *Jassa* did not consume macrophytes but preferred

epiphytic diatoms. The result was that macrophytes in aquaria with *Jassa* were clean after the duration of the experiment, whereas macrophytes with no *Jassa* were often covered by a heavy layer of epiphytes and diatoms. This suggests that *Jassa* may prevent epiphytism by removing spores, sporelings and diatoms from the surfaces of the macrophytes. Since food preferences had already been done on this species, *Jassa* was assumed to have no detrimental effects on South African *Gracilaria* and it was unnecessary to perform similar experiments.

Paridotea reticulata grows much larger in size than *Jassa*, up to 7.5cm (Kensley, 1978), and reached densities of up to 3 000 individuals per 100g dry *Gracilaria* (Smit, unpublished data). High densities of *Paridotea* had dry masses of up to 10g per 100g of *Gracilaria* in certain localities (Smit, unpublished data). Molloy (1992) also found large populations of *Paridotea* associated with *Gracilaria* in Luderitz, Namibia, where *Paridotea* reached over 20% of the total sample weight during the summer months and fell to almost negligible amounts during winter. Because these invertebrates can be so numerous, it is important to know the effects they may have on *Gracilaria*. As shown by numerous studies on the subject, the effects of grazers may be either detrimental (Nicotri, 1977; Shacklock and Croft, 1981) or beneficial (Howard and Short, 1986; Brawley and Fei, 1987; Duffy, 1990) to the crop, depending on the species of herbivore and alga.

Objectives

Food preferences and possible effects of *Paridotea reticulata* on commercially grown *Gracilaria* are unknown. The aim of this project was therefore to establish the effects that high densities of *Paridotea* may have on cultivated *Gracilaria* crops and associated epiphytes. Food preference experiments were performed on *Paridotea* to establish whether they preferred *Gracilaria* or the epiphytic *Ceramium*. In addition, feeding rate experiments were performed to establish an approximate rate of consumption on each of the seaweeds. Monthly samples of *Gracilaria* and associated flora and fauna were collected from *Gracilaria* rafts over the period of one year. No work was done on *Jassa* as there was no reason to believe that *Jassa* associated with *Gracilaria* in Saldanha Bay behave differently from those studied by Brawley and Fei (1987).

METHODS

Collection and storage of grazers and seaweeds

Netlons were pulled aboard a boat and suspended above buckets containing sea water, into which *Paridotea reticulta* of ranging size classes fell. Large *Paridotea* were also collected by SCUBA divers who picked *Paridotea* from the natural *Gracilaria* populations at Dias Rock (Northern shore of Saldanha Bay). Several hundred of these isopods were transported to a cold room in the University of Cape Town where they were left in aerated buckets. The cold room was maintained at a constant temperature of 15°C, a 16:8 light:dark photoperiod and a light intensity of $50\mu mol.m^{-2}.s^{-1}$. Isopods remained under these conditions for a period of three days before experiments commenced. During this time they were supplied with *Gracilaria gracilis* and *Ceramium sp.* and complete water changes were repeated approximately every third day. *Gracilaria* and *Ceramium* were also collected from the netlons and kept under similar conditions until they were needed for experimentation purposes.

Food Preference

Food choice experiments were performed on two isopod size classes. The animals of the large size class were on average 5.20 ± 0.16 cm, while those of the smaller class were 3.13 ± 0.07 cm in length.

Fragments of *Ceramium* and *Gracilaria* from Saldanha Bay were blotted dry and 0.20g of each was weighed out, thereafter they were placed together in a 650ml plastic container with sea water. Single isopods (*Paridotea*) were added to half of the containers after being weighed to two decimal places. Using single isopods eliminated any feeding bias which may have been caused by interactions (interference, aggression, etc.) between the consumers (Peterson and Renaud, 1989). The other half of the containers were controls and thus had no isopods. A total of 17 replicates were used for the smaller size class and 21 for the larger size class. These containers were placed in the 15°C storage room (referred to under "collection and storage of material") and left for 24 hours. The short duration of the experiment and small fragments of plant material ensured that mass change due to growth or decomposition were minimised (Peterson and Renaud, 1989).

After 24 hours, the seaweeds were removed from the containers, blotted dry and reweighed. Isopods were killed by freezing and their dry masses recorded after placing them in a drying oven (60°C) for three days. The differences in plant masses were calculated by subtracting the "mass after" from "mass before", thus giving the total mass consumed. Results obtained with the influence of consumers were compared to those without consumers (controls). Comparisons were made using t-tests for independent samples (STASTISTICA for Windows release 5.1, Statsoft Inc. 1984-1996) where the significance level was $p = 0.05$. Thus, the seaweed with the most significant mass loss would be the one favoured by *P. reticula.* Replicates where the isopod died or underwent ecdysis (moulting) were discarded.

Feeding Rates

Experimental conditions and procedure were similar to those of the food choice experiments, except *Paridotea* was only supplied with one seaweed (either *Ceramium* or *Gracilaria*) instead of both. Size classes used in experiments were 3.12 ± 0.14 cm and 5.22 ± 0.19 cm for *Ceramium* experiments and 3.16 ± 0.08 cm and 5.15 ± 0.14 cm for *Gracilaria* experiments. Mass differences between plants exposed to herbivore and controls were also compared using t-tests.

Consumption rates on Ceramium

Seventeen replicates were used for isopods of the smaller size and the mass of *Ceramium* used in each replicate was 0.20g. Twenty five *Ceramium* replicates were used for the larger size. The mass of *Ceramium* used per replicate was 0.30g because pilot experiments had indicated that large isopods are capable of eating in excess of 0.20g of *Ceramium* over the duration of 24 hours.

Consumption rates on Gracilaria

Sixteen replicates were used for smaller isopods and 0.20g of *Gracilaria* was placed in each container. The experiment lasted 24 hours. Twelve replicates were used for larger isopods. *Gracilaria* of 0.20g was placed in the containers and its mass recorded after 24 hours and again after one week.

Saldanha Bay Experiment

Twenty four 650ml, transparent, plastic containers were used in the experiment. Containers had panels cut out of them which were replaced with a very fine mesh (0.75 mm) to allow water to flow through the container. The mesh was fine enough to stop most invertebrate fauna from either entering or escaping. *Gracilaria* was blotted dry and 0.30g was weighed out and placed in each of the containers. *Gracilaria* fragments were suspended from a piece of string to prevent bumping against the container sides. Fifteen small *Paridotea* were placed in eight of the containers, whereas another eight containers each contained eight large *P. reticulata.* The remaining eight containers were controls containing no grazers added.

The small and large *Paridotea* size classes were 1.16 ± 0.02 cm and 2.19 ± 0.23 cm in length respectively. Isopod dry weights could only be determined after the experiment. The total mass of small and large isopods in each container were found to be similar (0.07 ± 0.01g and 0.08 ± 0.01g dry weight for small and large *Paridotea* respectively).

The containers were then suspended from a *Gracilaria* raft in Saldanha Bay at a depth of 0.5m from the surface and left for three days (3 June - 6 June, 1996). Water temperatures ranged from 13 to 14.5°C that time period. The weather was sunny with light wind for the first two days and became overcast and windy on day three. On the third day, the *Gracilaria* was removed and reweighed after blotting. Mass differences between the beginning and end of the experiment were compared and comparisons were made between the amount of *Gracilaria* eaten by small and large isopods These comparisons were made using ANOVA (STATISTICA for windows, release 5.1, Statsoft Inc. 1984 - 1996). Isopod dry weights were determined by placing the dead isopods in a 60°C drying oven for three days and weighing them to two decimal places.

This experiment attempted to establish the amount of *Gracilaria* consumed by *Paridotea* in its natural environment. Although isopods were exposed to natural circadian rhythms, swell conditions, water temperatures and water flow, some of the natural conditions could not be simulated. Isopods were still rather "exposed" because they were supplied with only a small fragment of Gracilaria in contrast to the large

quantities of seaweed cover found in raft populations. Isopods were also enclosed in plastic containers instead of being free swimming. The experiment was not repeated using *Ceramium* as there was very little of the epiphyte available during the month of June 1996.

Population Dynamics of *Paridotea*, *Ceramium* and *Gracilaria*

Epiphyte and grazer infestations of *Gracilaria* grown on a suspended seaweed raft in Saldanha Bay were determined at monthly intervals, excluding the months of June and July. A diver randomly removed six replicate samples of *Gracilaria* from a netlon and placed them into 650ml, plastic honey jars with screw-on lids. Normally a replicate sample consisted of a single tuft but occasionally when the seaweed material was of poor quality, it comprised of clumps broken off several plants. On the boat, the samples were preserved in approximately 4% formaldehyde in seawater and stored until it could be sorted back in the laboratory, often several months after collection.

The samples were sorted into the following: infertile *Ceramium*, *Gracilaria*, *Paridotea* and other crustaceans, usually a combination of amphipods, copepods and stomatopods. Few attempts were made to distinguish between the last three crustacean groups and they were normally clumped in a single category. Griffiths (pers. comm.) sorted one sample and identified 95% of this miscellaneous crustacean group as *Jassa*. Subsequently, three other samples were analysed, they too contained in excess of 90% *Jassa*. Mass and numbers of epiphytes were standardised to g(dry mass) *Ceramium* or *Paridotea*, or number of *Paridotea* per 100g(dry mass) *Gracilaria* or *Ceramium*, or per 100g(dry mass) total plant material. The dry mass of isopods was not recorded for the month of August.

RESULTS

Food Preference

Large *Paridotea* has a marked preference for *Ceramium* (Figure 2.). Grazed *Ceramium* suffered a significant biomass loss (0.13 ± 0.05g) in contrast to the biomass gains of the controls (0.01 ± 0.01g; $p < 0.05$). Although these isopods had equal access to *Gracilaria*, *Gracilaria* in food choice experiments lost 0.00 ± 0.02g

while the control plants gained 0.00 ± 0.02g of biomass. This biomass loss was insignificant, $p > 0.05$. Thus, when offered the choice of *Ceramium* or *Gracilaria*, large isopods chose *Ceramium*.

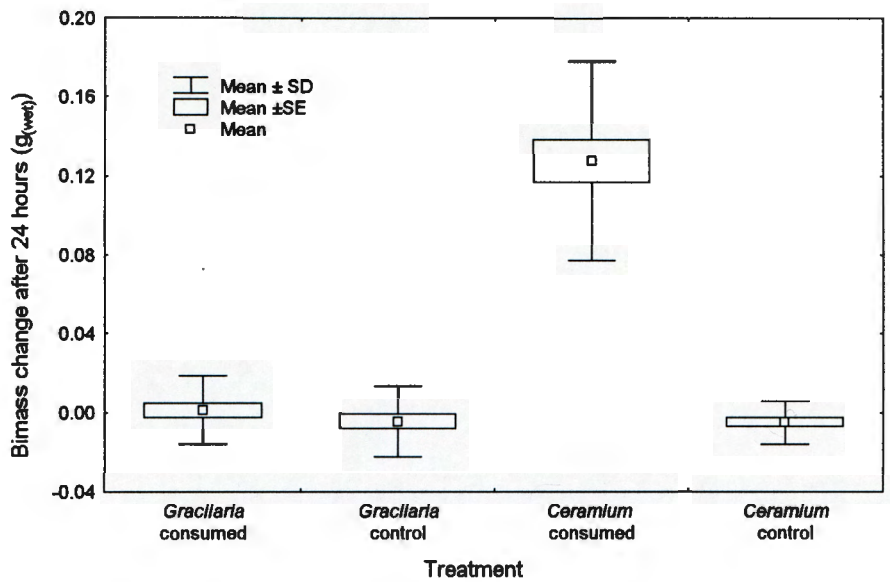

Figure 2. Food choice of large isopods over 24 hours.

Figure 3. clearly indicates that small isopods also have a marked preference for *Ceramium*. *Ceramium* suffered large biomass losses due to grazing (of 0.03 ± 0.03g) in contrast to the biomass gains of the controls (0.00 ± 0.01g). This difference was significant ($p < 0.05$)."Grazed" *Gracilaria* and control *Gracilaria* both gained biomass of 0.00 ± 0.02g and 0.00 ± 0.01g respectively ($p > 0.05$). Therefore there was no significant difference between *Gracilaria* exposed to isopods and *Gracilaria* controls. Thus, when offered the choice of *Ceramium* or *Gracilaria*, small isopods chose *Ceramium*. Thus, size class (between 3.13 ± 0.07 and 5.20 ± 0.16cm) does not influence the choice of food.

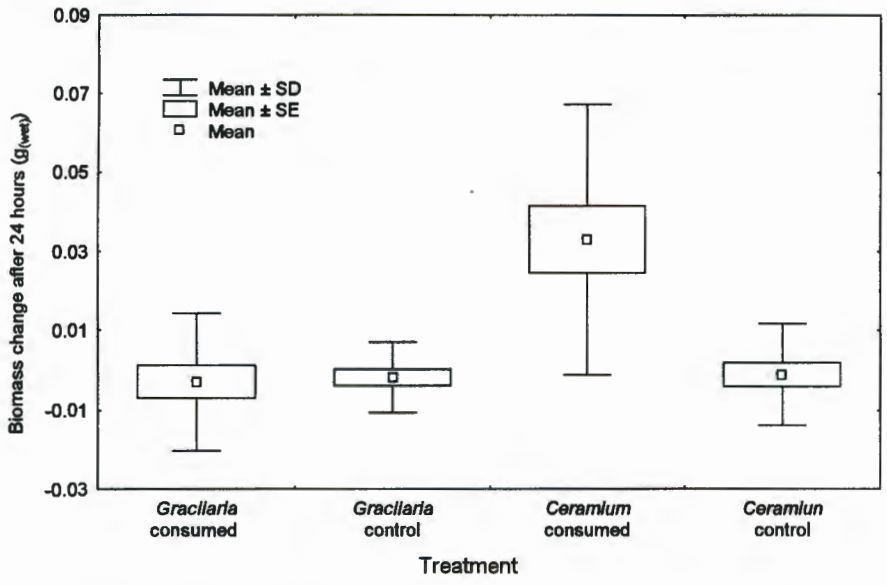

Figure 3. Food choice of small isopods over 24 hours.

Feeding Rates

Consumption rates on Ceramium

Ceramium lost significant biomass after being exposed to small isopods for 24 hours (Figure 4). Biomass loss due to herbivory was 0.03 ± 0.02g, while controls showed a mean biomass loss of 0.00 ± 0.01g. The difference in biomass loss between the controls and grazed samples was significant ($p < 0.05$). Thus, small isopods of 0.05 ± 0.01g dry mass are capable of consuming 0.03 ± 0.02g *Ceramium* (wet) per day. This is 0.67 ± 0.58g *Ceramium* (wet) consumed per dry gram of *Paridotea* per day.

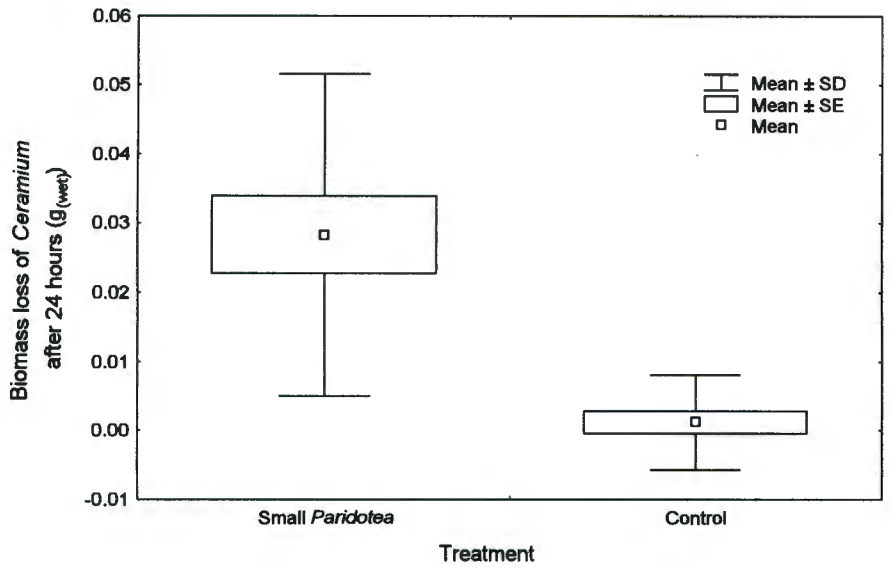

Figure 4. Biomass of *Ceramium* lost after exposing 0.20g wet weight to small isopods and controls for 24 hours.

Ceramium underwent a significant ($p < 0.05$) loss of biomass (Figure 5.) after being exposed to the feeding pressure of a large *Paridotea* for 24 hours. The mean biomass lost was 0.12 ± 0.07g which was significantly different from the control at 0.00 ± 0.02g ($p < 0.05$). Thus, in 24 hours 0.28 ± 0.03g of large isopods (dry mass) are capable of consuming approximately 0.12 ± 0.07g *Ceramium* (wet). This is 0.44 ± 0.24g of *Ceramium* consumed per dry gram of isopod in 24 hours.

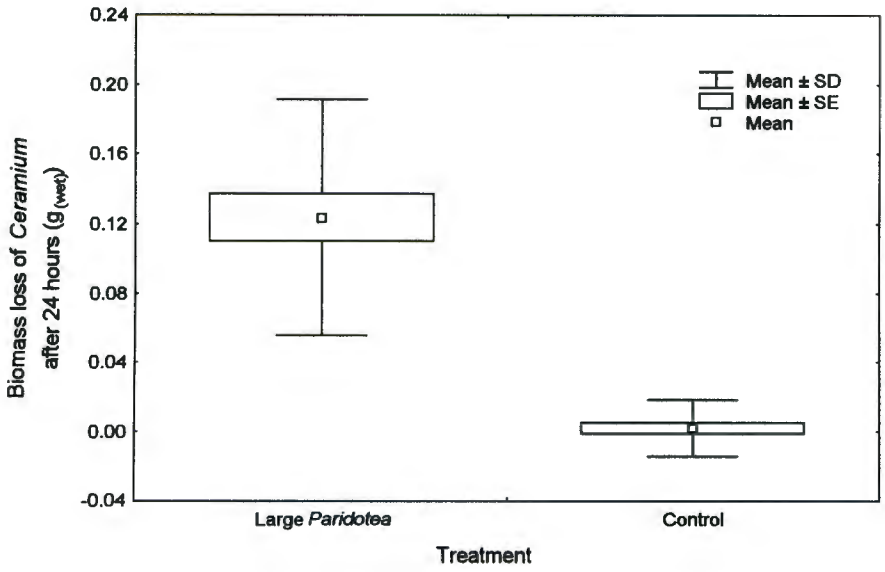

Figure 5. Biomass of *Ceramium* lost after exposing 0.30g wet weight to large isopods and controls for 24 hours.

Consumption rates on Gracilaria

Small *Paridotea* had little or no effect on the biomass of *Gracilaria* over 24 hours (Figure 6). After the duration of the experiment, "grazed" plants had lost 0.00 ± 0.02g, while the control plants gained 0.00 ± 0.01g. This small difference between grazed and control plants was insignificant ($p > 0.05$).

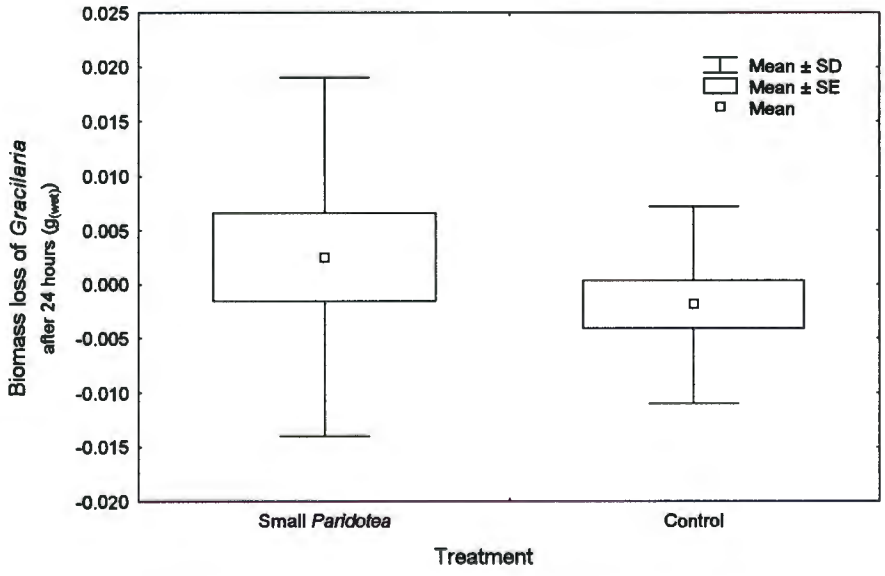

Figure 6. *Gracilaria* loss after exposing 0.20g to small isopod grazing for 24 hours.

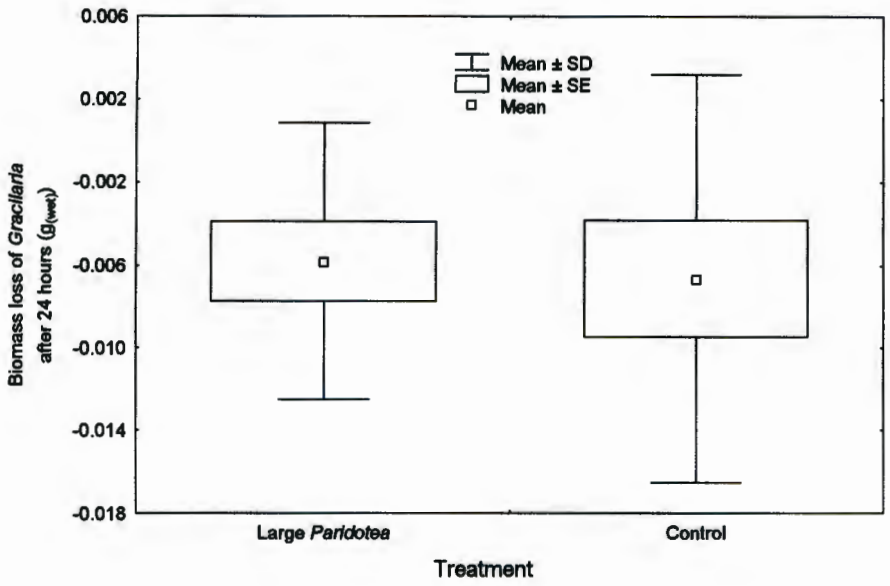

Figure 7. Biomass of *Gracilaria* lost after exposure to large isopods for 24 hours.

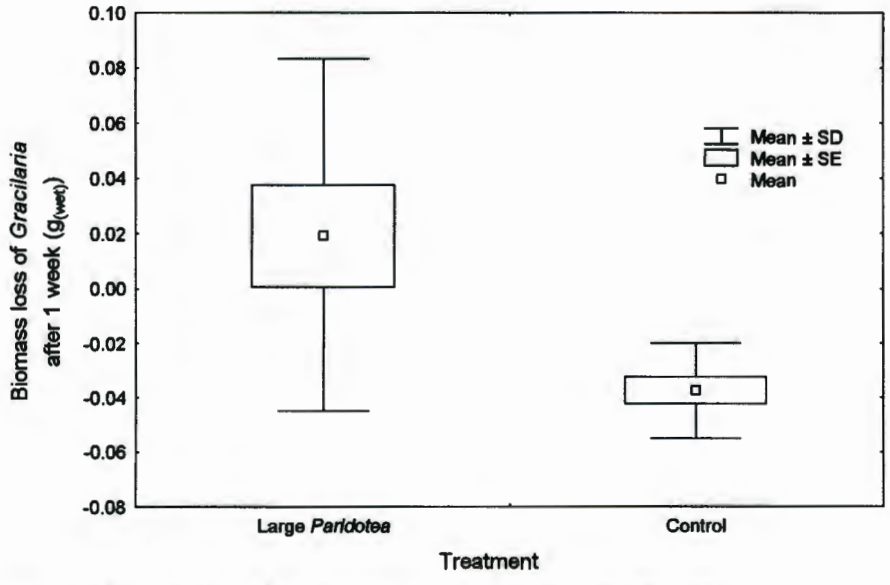

Figure 8. Biomass loss after exposure to large isopods for one week.

Saldanha Bay Experiment

The addition of isopods had no effect on the biomass of *Gracilaria* in this experiment (Figure 9). The biomass changes were the same for the small and large isopod classes, as they were for control experiments ($p > 0.05$). *Gracilaria* in all treatments gained biomass (0.02 ± 0.02) for both isopod treatments and 0.03 ± 0.02 for controls).

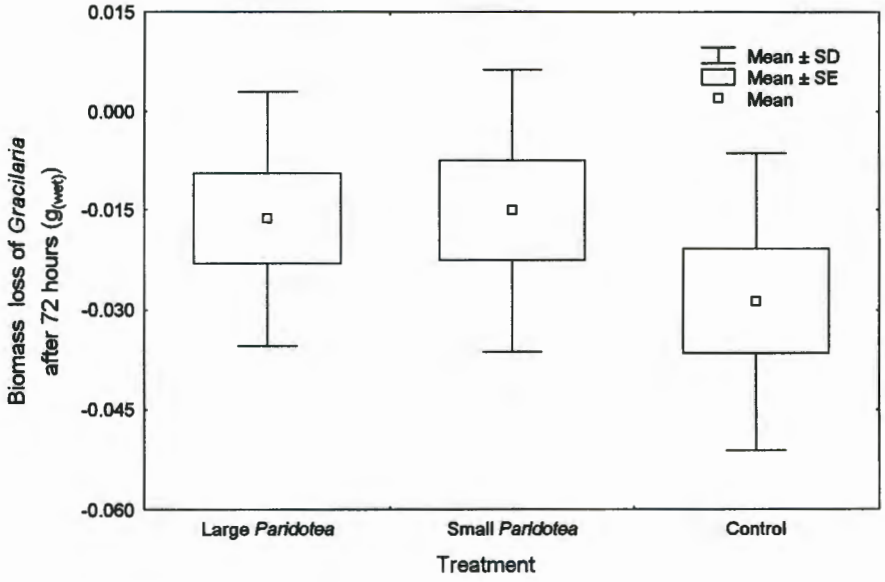

Figure 9. Biomass of *Gracilaria* lost after being exposed to three different herbivory treatments in Saldanha Bay.

Population Dynamics of *Paridotea*, *Ceramium* and *Gracilaria*

Paridotea was be found on the *Gracilaria* raft throughout the months sampled, even when *Ceramium* populations are very low or absent (Figures 11 and 12). The numbers and dry mass of *Paridotea* matched the abundance of their principal food source, *Ceramium* fairly well (Figures 11 and 12). Although the strength of the relationship was not very strong ($R^2 = 0.52$ and 0.56 respectively), the relationship were still statistically significant ($p < 0.05$). During September, the *Paridotea* population reaches a maximum as does the percentage *Ceramium*, before falling again in October. During October, November and December, *Ceramium* populations are very low, while *Paridotea* begins to climb slowly. Paridotea and *Ceramium* populations peak for a second time together during the month of *February*. The following month sees the simultaneous collapse of both *Paridotea* and *Ceramium*.

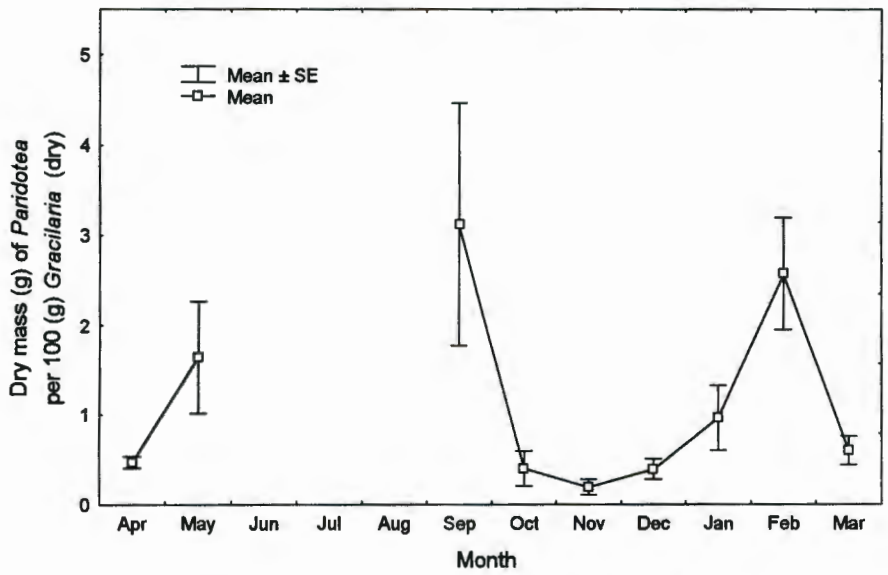

Figure 10. Dry mass of *Paridotea* per 100g of *Gracilaria* over the period between April 1995 and March 1996.

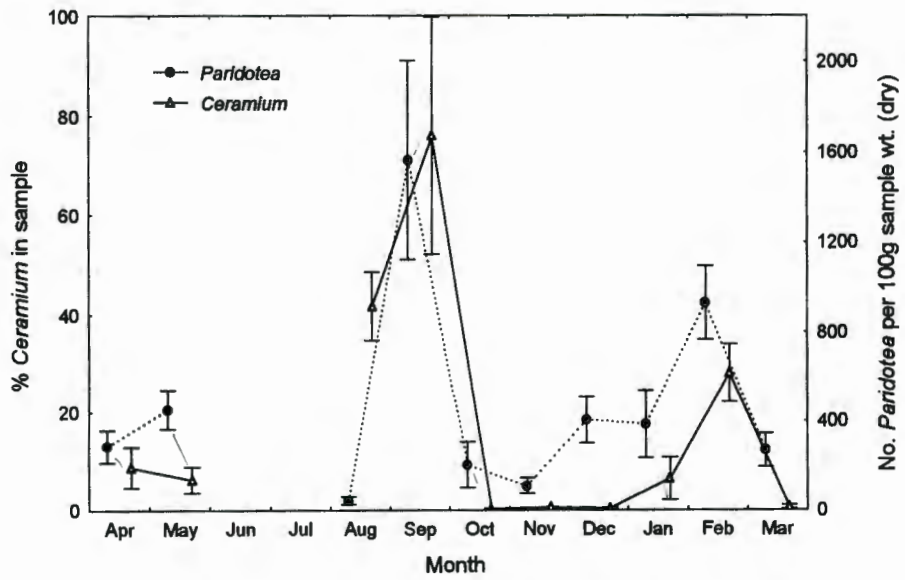

Figure 11. Percentage *Ceramiun* per sample and number of *Paridotea* per 100g of sample weight over the period April 1995 to March 1996 in Saldanha Bay. Data points are monthly averages (n = 6) and vertical bars are standard errors.

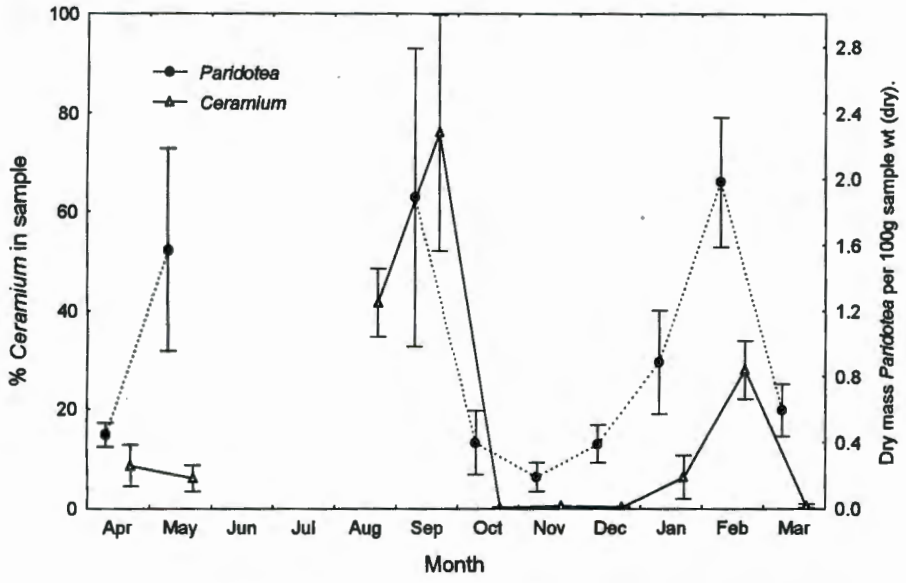

Figure 12. Paridotea biomass and percentage Ceramium per 100g of sample over the period April 1995 to March 1996 in Saldanha Bay. Data points are monthly averages (n = 6) and vertical bars are standard errors.

Paridotea biomass reaches a maximum of 4.5g dry mass per 100g *Gracilaria* (Figure 10). However, the grazing pressure on *Gracilaria* during these months is probably minimal due to the abundance of the preferred food *Ceramium* (Figures 11 and 12). Months which had little or no *Ceramium* were October, November, December and March (Figures 11 and 12). During these months the *Paridotea* may be forced to feed on *Gracilaria*. However, the *Paridotea* population remained low during these months peaking with a maximum of 0.6g. dry mass per 100g dry mass of *Gracilaria* in October.

The possible daily consumption of *Ceramium* was calculated for each month using the rate of 0.67g consumed per dry gram of *Paridotea*. This was the rate calculated for small isopods in feeding rate experiments on *Ceramium*. The daily consumption of *Ceramium* was negligible when *Ceramium* populations were high because *P. reticulata* biomass was relatively low (Table 1). The percentage of *Ceramium* consumed is generally much higher when *Ceramium* populations are low (Table 1). Biomass loss of this magnitude could seriously retard the growth and spread of *Ceramium*.

Table 1. The percentage *Ceramium* found in samples throughout the year and the percentage *Ceramium* consumed daily. Consumption rates are calculated using the rate of 0.44g. *Ceramium* (dry weight) consumed per gram of *P. reticulata* (dry weight).

	Percentage *Ceramium* in samples	Dry mass of *Paridotea* per 100g. *Ceramium*	Percentage *of Ceramium* consumed in sample
Apr '95	8.68%	0.42g.	0.53
May '95	6.18%	0.43g.	2.03
Sep '95	76.00%	0.14g.	0.30
Oct '95	0.27%	12.33g.	11.20
Nov '95	0.61%	3.03g.	2.41
Dec '95	0.40%	8.43g.	7.45
Jan '96	6.44%	0.75g.	1.23
Feb '96	27.98%	0.19g.	0.74
Mar '96	.68%	4.92g.	8.76

DISCUSSION

Isopods of two size classes studied have a preference for *Ceramium* over *Gracilaria* When offered no choice at all, isopods still consumed little or no *Gracilaria* over a period of 24 hours. However, when isopods were left with only *Gracilaria* for long periods, evidence of herbivory was evident. This herbivory may only be detectable on *Gracilaria* after a long period of time because isopods consume *Gracilaria* at a very slow rate. Alternatively, over a long period, they become starved of *Ceramium* and are forced to consume *Gracilaria*.

Isopods were found in all months when samples were collected on the *Gracilaria* rafts and their greatest biomass corresponded to those months with large *Ceramium* populations. Their lowest biomass generally corresponded to months with small populations of *Ceramium* This indicates that isopod numbers may be regulated at a given locality depending on food availability. These responses are probably due to immigration from areas with sparse epiphyte populations. These epiphyte poor areas may include the natural population situated on the sea floor. Because natural populations are located on the sea floor (about 0.5 - 6m from the surface), light and temperature conditions differ from those on the raft. As a result epiphyte populations differed between the raft and the natural population (pers. obs). It would be interesting

to conduct population dynamics experiments on the flora and fauna of both the raft and the natural population for the period of a year to see how they differ. It is unlikely that large increases in isopod biomass are due to reproduction alone because these increases occur in the time span of less than one month.

Impact on *Gracilaria*

During the months of October, November, December and March when *Ceramium* was scarce, *Paridotea* was still fairly abundant. During these months, isopod biomass was low relative to *Gracilaria*. This, coupled with *Paridoteas'* strong preference for *Ceramium*, implies that grazing pressure on *Gracilaria* should be very low. During May, September and February, *Paridotea* biomass was high in relation to *Gracilaria*. However, the grazing pressure on *Gracilaria* was still minimal because during these months there were large populations of *Ceramium* on which the isopods were more likely to feed.

It seems that isopods have a positive effect on *Gracilaria* by decreasing its epiphyte load. However, this decrease in epiphyte load may not be enough to cause a significant increase in *Gracilaria* productivity.

Impact on *Ceramium*

The periods where *Ceramium* populations are low, probably correspond to environmental conditions which are not perfect for *Ceramium* growth. *Ceramium* growth rates may be slower due to unfavourable temperature or light conditions. *Paridotea* populations are relatively high when *Ceramium* populations are low and vice versa. Thus, the grazing effects of *P. reticulata* are more important when *Ceramium* populations are low. For example, it was calculated that 11.2 % of the total *Ceramium* population could be consumed in one day by isopods feeding at the rates calculated by feeding rate experiments. However, the daily percentages of *Ceramium* grazed are very approximate values as they were extrapolated from laboratory experiments and applied to field data. However they do indicate that grazing by isopods is potentially important during the months of March, October and December,

when *Ceramium* populations are low. Feeding rates may fall during these months of low epiphyte abundance due to *Paridotea*'s inability to find *Ceramium* and isopods may also start using *Gracilaria* as an alternative food source. It would be interesting to perform gut content analyses on isopods throughout the year, noting how their diets correspond to the availability of the different food sources at the time. Despite possible fluctuations in feeding rates due to temperature or abundance of grazing material, the greatest herbivore pressure probably still exists during the months when *Ceramium* is scarce. If *Ceramium* populations are sparse during some months, primarily due to unfavourable environmental conditions, then the effects of slow growth rates and high grazing rates could be very detrimental to *Ceramium*.

The effects of grazing are probably unimportant when *Ceramium* populations are high (e.g. in September 1995). Here, biomass lost daily due to grazing was calculated as a fraction of a percentage of the total *Ceramium* biomass. In addition the huge *Ceramium* populations are probably large because they are growing under favourable growth conditions. Thus, the months of January, February, April and September were characterised by large *Ceramium* populations, low herbivory levels and possibly high growth rates.

Factors Influencing Herbivore Preference

There are several reasons for herbivores food preference (Nicotri, 1980), e.g. calorific value, chemical defence and morphology. Measurements of water content, caloric contents or nitrogen contents are all factors which may influence the final choice of a potential grazer selecting its food depending on energy content. The functional-form model of Littler (1980), suggests that highly branched growth forms have a higher calorific value than more simple growth forms. The morphology of *Gracilaria gracilis* and *Ceramium* sp. are very different with *Ceramium* being delicate and very finely branched, while the branches of *G. gracilis* are sparsely branched. Thus, *Paridotea* may choose *Ceramium* over *Gracilaria* on the basis of calorific values. A host of literature is available on the effects of chemical defences on food preference (e.g. Hay and Fenical, 1988; Tugwell and Branch, 1989; Poore, 1994) but very little is mentioned about either *Gracilaria* or *Ceramium*. Chemical concentrations may vary

within a plant and are often found in higher concentrations in the meristematic regions or reproductive regions. As a result, lower levels of herbivory may take place in these heavily protected regions. Chemical differences may also vary from species to species with herbivores often preferring those plants that are poorly protected (e.g. Steinberg, 1985 and Poore, 1994). Perhaps this is part of the reason for *Paridotea's* preference in favour of *Ceramium*. An unidentified species of *Gracilaria* contains an anti herbivore compound, acetogenin (Hay and Fenical, 1988). There are no references indicating the presence of anti herbivore compounds in the genus *Ceramium*. In addition, Littler (1980) identified finely branched species as having fast growth rates and as being dependent on intense light. These characteristics are associated with low levels of chemical defence in terrestrial plants (Coley et al., 1988; Coley, 1988). Thus, the same theory may be true for algae, leaving *Ceramium* sp. less heavily defended than *G. gracilis*. Littler (1980) also postulates that coarsely branched growth forms are tougher than finely branched growth forms. For this reason, *Ceramium* may be the preferred food source because is easier to graze or even digest.

Implications for Mariculture

It may be difficult to use the results obtained to improve the yields or quality of *Gracilaria* produced by the present forms of open water mariculture in South Africa. The manipulation of isopod biomass in open water mariculture would probably be a rather difficult process because any animals introduced would soon disperse. However, if tank culture techniques were to become popularised in South Africa, it may be easy to reduce epiphyte loads by manipulating environmental conditions in conjunction with herbivore levels.

Conclusion

If isopods are not present on Gracilaria rafts, *Ceramium* may be able to quickly reach pest status, even when environmental conditions are not perfect for its growth. However, during certain times of year, environmental conditions may favour the rapid growth of *Ceramium*. During these months, growth is so rapid, that isopods are largely ineffectual in combating the spread of *Ceramium*. Isopods do respond to increases in